Spermathecal Structure in Canthyporus Zimmermann (Coleoptera, Dytiscidae)

by P. Mazzoldi

Abstract: The structure of the spermatheca and its relations with the other female genital organs are studied in nine species of the genus *Canthyporus* Zimmermann. Although the general plan of the female genitalia is substantially uniform within the genus, there are marked variations in size and shape of the spermatheca, in its degree of sclerotisation and in the length of the spermathecal duct between the different species. The female genitalia of *Canthyporus* are compared with those of other Hydroporinae, and some phylogenetic considerations are advanced. Comparison of these characters with others found in *Canthyporus* (presence of a projection on the aedeagus, shape of parameres and presence of metasternal lines) allows identification of different phyletic lineages within the genus.

Key words: *Canthyporus*, Dytiscidae, spermatheca, phylogeny.

Introduction

Although the study of the male genitalia for diagnostic and phylogenetic purposes has a long tradition in coleopterology, the study of the female genital organs was until recently neglected; this happened because they were supposed to have less taxonomic importance, since they are less sclerotised and show less interspecific variation. This situation has now begun to change: BURMEISTER (1976) used the female genitalia for phylogenetic analysis; ORDISH (1985) drew attention to the possible diagnostic importance of the spermatheca in New Zealand Dytiscidae; ANGUS (1985), on the basis of spermathecal structure, separated *Suphrodytes* from *Hydroporus*, and FERY (1992a and 1992b) used gonocoxae and gonocoxosterna for species identification in his works on the genus *Coelambus;* more recently, DEUVE (1993) produced a very detailed study of the female genitalia in Adephaga, although this last work concentrates mainly on terrestrial families. Despite this very little is known about the female genitalia of most genera. At the end of 1991 – beginning of 1992 I visited Cape Province, South Africa and collected water beetles, including a number of species of *Canthyporus*. This genus, exclusive to the Ethiopic region, includes 30 species today, 23 of which are distributed in South Africa, with a high concentration in the Cape Province (J. OMER-COOPER 1955, 1956 and 1965). Six are scattered on the mountains of central Africa (WEWALKA 1981 and

NILSSON 1991) and one is found in Madagascar (GUIGNOT 1959). The study of the specimens I collected revealed the presence of very interesting spermathecae, an aspect which had so far been overlooked in this genus. As I think that these structures may help in species identification and may also have phylogenetic importance, I describe in the present paper the spermathecae of the nine species of *Canthyporus* which were available to me.

Materials and methods

All the beetles used for this study were collected by me, killed with ethyl acetate and preserved in alcohol until I dissected them. The usual method employed for the extraction of male genitalia, pulling them out through the abdominal opening with tweezers or pins, is not suited to study of the female genitalia, since these more delicate structures are usually damaged by this procedure, and lose their original anatomical connections and orientation. Therefore, I devised the following method, which is, with slight modifications, the same as that employed by BRANCUCCI (1980) in his study on Cantharidae: by inserting a handled micro – pin between the fifth and sixth ventrites, the last part of the abdomen was removed and then placed in a drop of water. Working carefully with micro – pins, the terga were cut away, the last part of the gut was turned backward and then torn off, and finally the ventrites were removed. The isolated piece was macerated in a 10% solution of KOH for 10–12 hours and then coloured with May-Grünwald. At this point the female genitalia were visible in their original orientation; they were then placed in a drop of glycerol and drawn using a stereo-microscope fitted with a camera lucida; observations were also made with an optical microscope.

All the drawings show the genitalia in dorsal view; care was taken to draw the parts, as far as possible, in their original orientation, although the spermathecal duct, which was originally folded over the spermatheca, was turned to the right to allow easier examination of the latter organ, especially in the species with a very long duct. The position of the gonocoxae and gonocoxosterna relative to the other parts was sometimes influenced by the extraction procedure, since this caused a greater or lesser distension of the ligaments connecting these parts to the terminal part of the vagina and bursa copulatrix. One must also note that while the shape of the sclerotised parts (e.g. spermatheca, gonocoxae, gonocoxosterna) is substantially stable, the

same cannot be said of the soft parts, such as the vagina, bursa copulatrix and oviducts, whose shape and state of extension may have been influenced both by the conservation and extraction procedures, and by the physiological state of the organs. It is obvious that the physiological state of the female (time of copulation, position of spermatophore and fertilisation) must have some influence on the status of these organs, and in order to take this into consideration 6–7 specimens were dissected for each species (when sufficient females were available); nonetheless, no differences between specimens of the same species were observed, except for minor ones concerning the folding of the spermatheca and the first stretch of the spermathecal duct. This uniformity is probably due to the fact that all the specimens were collected in a single, very short period of the year, and were therefore in the same reproductive state.

After drawing, the pieces were mounted in DMHF employing the technique described by BAMEUL (1990) and pinned together with the insects. All the specimens used for this study are kept in my collection.

I have considered the following nine species of *Canthyporus*, listed here with the localities where they were collected, all in the western Cape Province of South Africa. For each species the number of females dissected is indicated between brackets:

Canthyporus canthydroides Régimbart: Somerset West, marshy area near Firgrove, 28–29 december 1991 (6 exx.)

Canthyporus testaceus Zimmermann: Cape Agulhas, Soetendalsvlei, 1 january 1992 (4 exx.).

Canthyporus navigator Guignot: Somerset West, marshy area near Firgrove, 28–29 december 1991 (6 exx.)

Canthyporus guignoti J. Omer-Cooper: small stream near Theewaterskloof Dam, 31 december 1991 (3 exx.)

Canthyporus latus J. Omer-Cooper: Du Toits river near Franschhoekpas, m 450, 31 december 1991 (2 exx.)

Canthyporus hottentotus Gemminger & Harold: Somerset West, marshy area near Firgrove, 28–29 december 1991 (6 exx.)

Canthyporus petulans Guignot: small stream near Theewaterskloof Dam, 31 december 1991 (7 exx.)

Canthyporus consuetus J. Omer-Cooper: small stream near Theewaterskloof Dam, 31 december 1991 (2 exx.)

Canthyporus lowryi J. Omer-Cooper: small stream near Theewaterskloof Dam, 31 december 1991 (7 exx.).

The record of *C. guignoti* is the most interesting in the list, since this species was previously known only from the Eastern Cape

(OMER-COOPER in his paper of 1965 sets the border between Eastern and Western Cape at a line drawn from the mouth of the Storms River north to the Orange River).

In order to compare the female genitalia in *Canthyporus* with other genera, I have also dissected, with the same techniques, a number of other species of Dytiscidae: *Copelatus caffer* Balfour – Browne, *Celina angustata* Aubé, *Laccornis oblongus* (Steph.), *Hydrovatus pustulatus* Melsh., *Hydroglyphus pusillus* (F.), *Nebrioporus suavis* (Sharp), *Deronectes hispanicus* (Ros.), *D. moestus* Fairm., *Suphrodytes dorsalis* (F.) and *Hydroporus palustris* (L.)

Results

Although there are variations in the different species, the general structure of the female genitalia appears substantially uniform in the genus as can be seen from figures 1–9. The spermatheca is linked by a rather long spermathecal duct to a bursa copulatrix, and by a relatively short fertilisation duct to the vagina, which in turn is connected to the common oviduct. The surface of the spermatheca is covered by a number of glands (I have called them appended glands accepting the term proposed by Deuve (1993), although I am not totally sure that these structure are really homologous, since in the terrestrial Adephaga studied by Deuve there is, when present, only one gland connected to the spermatheca, while in Hydroporinae there are many small glands covering the surface of the spermatheca); these glands cover the terminal part of the spermatheca and sometimes the fertilisation ducts. The vagina and bursa copulatrix open externally with two independent openings, one behind the other. The vagina is connected to the common oviduct, which can be easily distinguished when examined under the microscope, since its external surface is covered by sclerotised spines. The interspecific variations concern mainly the size and shape of the spermatheca, its degree of sclerotisation, the length of the spermathecal duct and the size and number of appended glands; gonocoxae and gonocoxosterna also vary in shape, especially the former. It must be noted that some organs present in this area of the body have not been figured in the drawings for reasons of clarity, as they would partially cover the genitalia. This concerns mainly the pygidial glands with their tanks and the muscular bundles (there are evident muscular bundles connecting the proximal tip of the gonocoxae to the distal tip of the gonocoxosterna and to the bursa copulatrix).

In the following sections I give a description of the female genitalia in the nine species of *Canthyporus* studied.

Canthyporus guignoti J. Omer-Cooper   Fig. 1.

Spermatheca small, formed of an S-shaped tube with a kind of "cap"; weakly sclerotised. Fertilisation duct very short, spermathecal duct very long and thin, coiled, non-sclerotised. Appended glands small, covering part of the spermatheca and the fertilization duct. Bursa copulatrix rather large, non-sclerotised.

Fig. 1: Spermatheca and related organs in *Canthyporus guignoti*. Ov: oviducts; sp: spermatheca; gl: appended glands; sd: spermathecal duct; fd: fertilisation duct; vg: vagina; bc: bursa copulatrix; gc: gonocoxae; gs: gonocoxosterna.

598 P. Mazzoldi

Canthyporus navigator Guignot Fig. 2.

Female genitalia very similar to those of *C. guignoti*.

Fig. 2: Spermatheca and related organs in *Canthyporus navigator* Guignot.

Canthyporus canthydroides Régimbart   Fig. 3.

Spermatheca rather large, dilated, weakly sclerotised. Fertili-sation duct very short, spermathecal duct relatively short and thicker than in *C. navigator* and *C. guignoti,* non coiled, non-sclero-tised. Appended glands small, covering part of the spermatheca and the fertilisation duct. Bursa copulatrix rather large, non-scle-rotised.
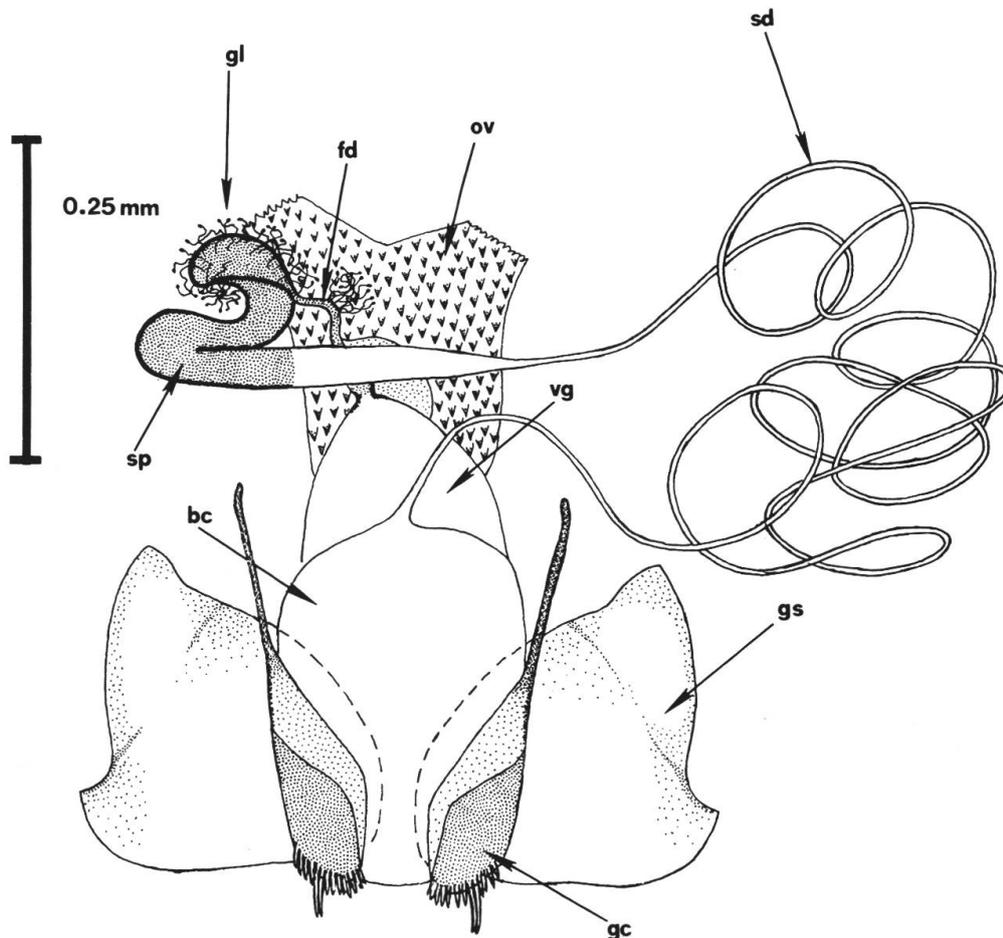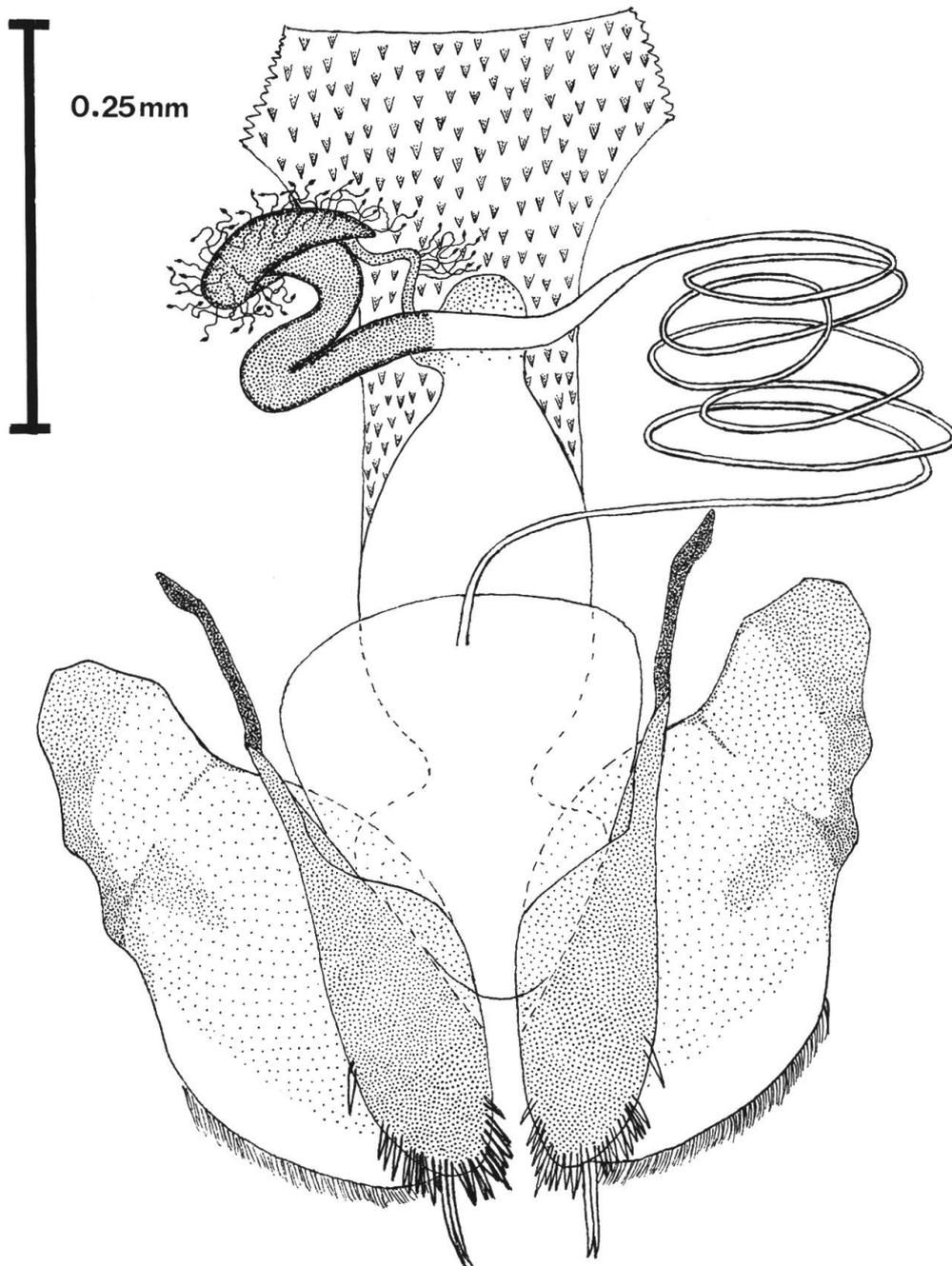

0.25 mm
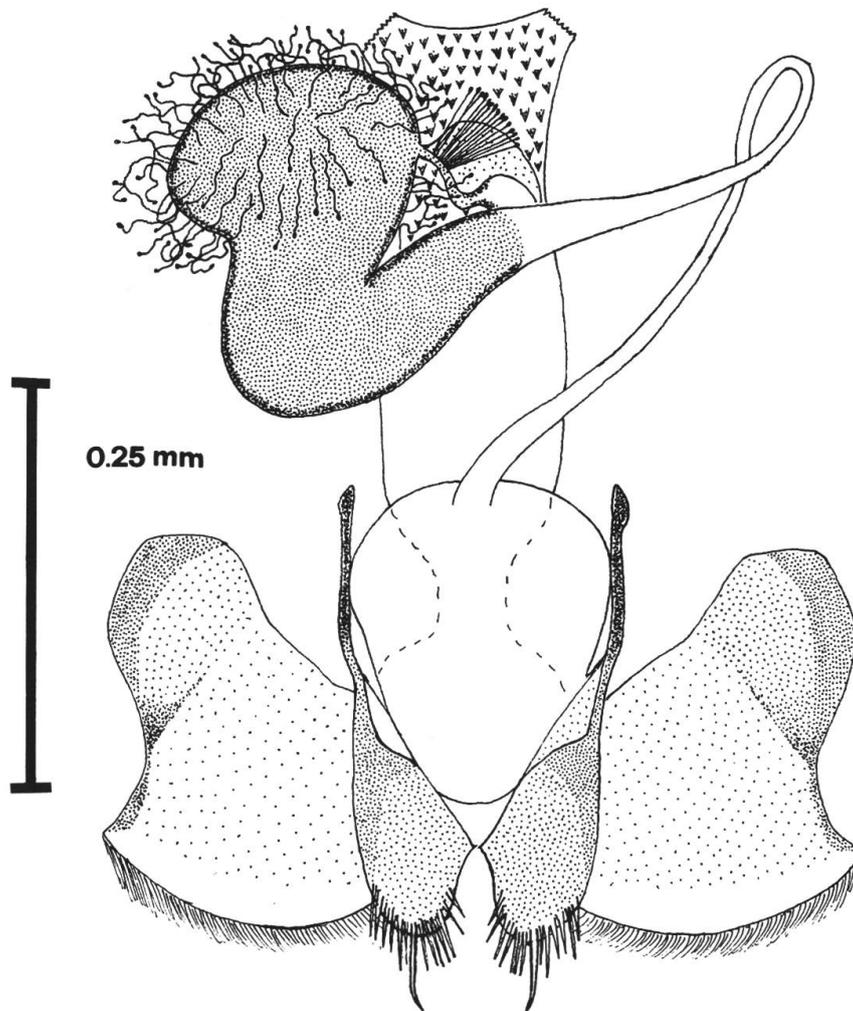
Fig. 3: Spermatheca and related organs in *Canthyporus canthydroides* Régim-bart.

Canthyporus testaceus Zimmermann   Fig. 4.

Spermatheca as in *C. canthydroides,* fertilisation duct very short. Spermathecal duct relatively short and very thick, non-coiled and non-sclerotised. Fertilisation duct short. Appended glands small, covering part of the spermatheca and the fertilisation duct. Bursa copulatrix large, non sclerotised.
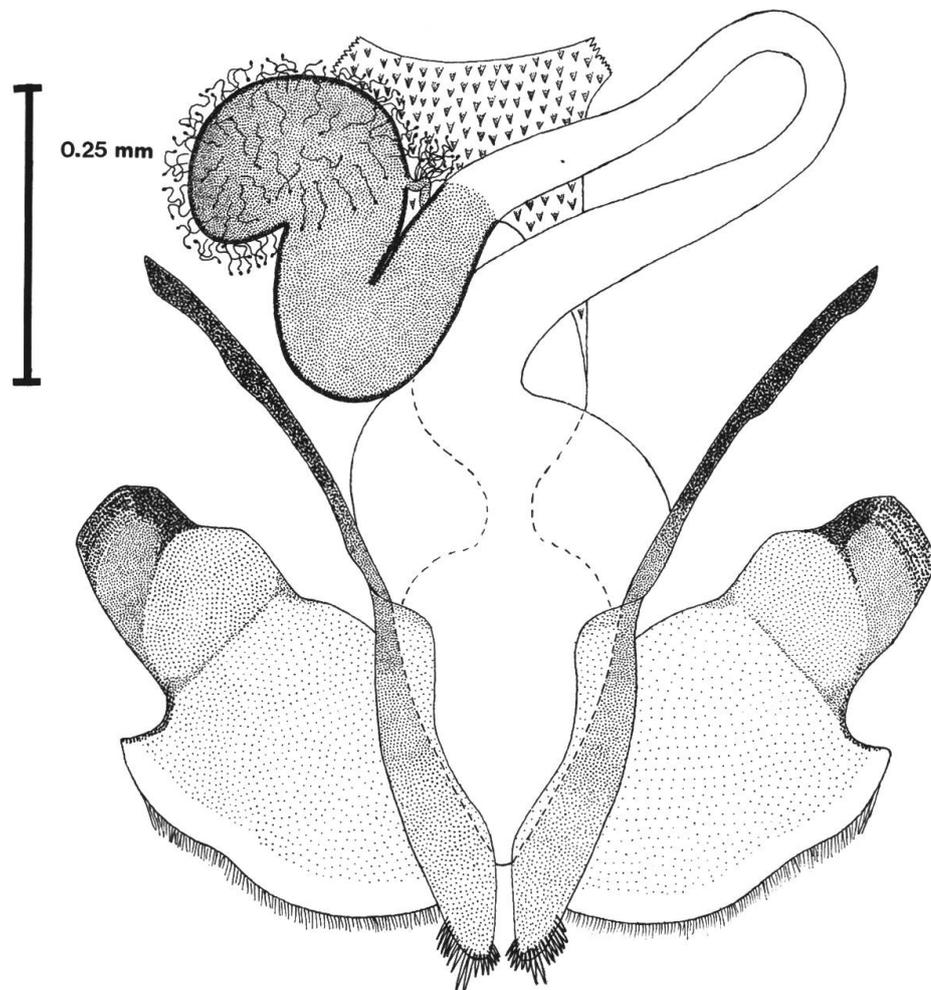
Fig. 4: Spermatheca and related organs in *Canthyporus testaceus* Zimmermann.

Canthyporus hottentotus Gemminger & Harold   Fig. 5.

Spermatheca rather large but not very dilated, formed by a hook- shaped tube connected by a sharp bend to a straight one, in part strongly sclerotised (the hook) in part less strongly sclerotised with a non-sclerotised stretch interposed. Spermathecal duct moderately long and thick, weakly sclerotised, weakly coiled; fertilisation duct short. Appended glands small, covering part of the spermatheca.
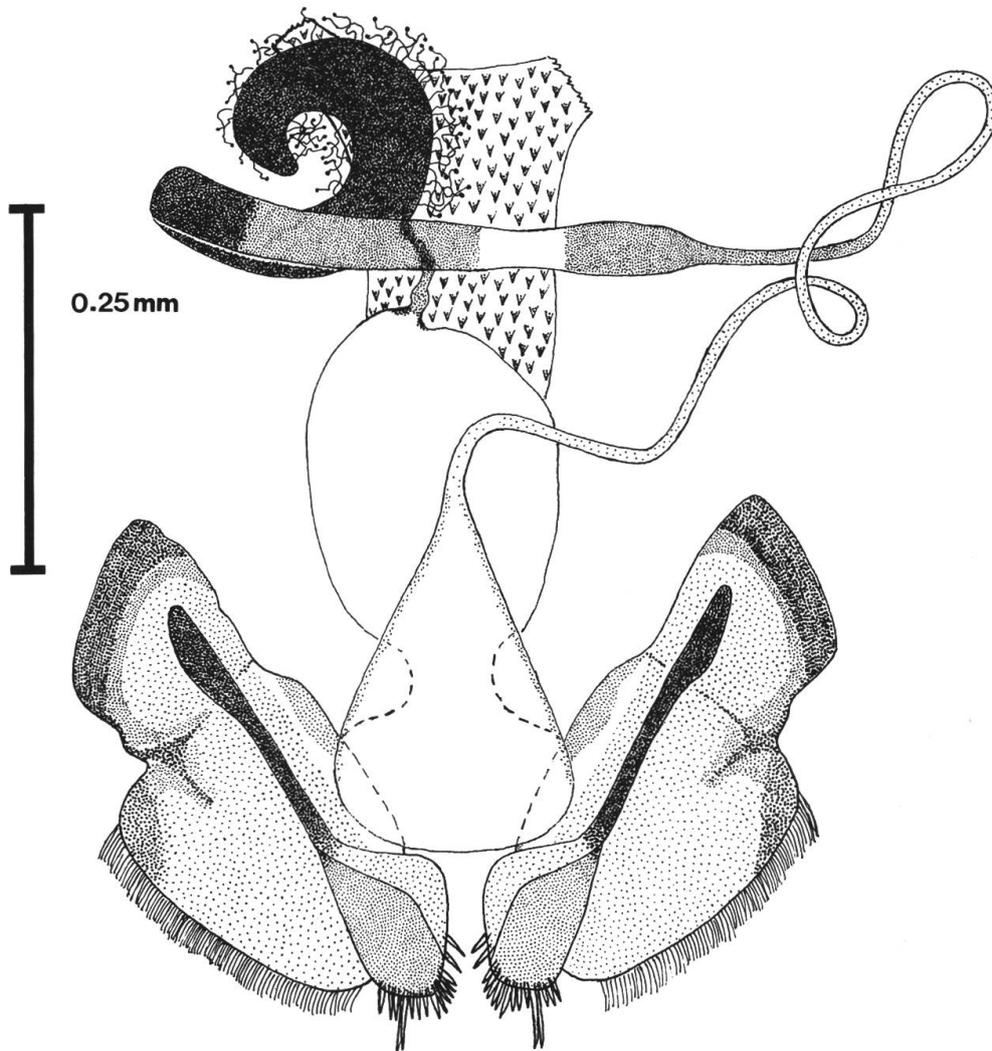
Fig. 5: Spermatheca and related organs in *Canthyporus hottentotus* Gemm. & Har.

Canthyporus petulans Guignot Fig. 6.

Spermatheca as in *C. hottentotus,* only the tube forms a more complex bend (see figure). Spermathecal duct slightly shorter than in *C. hottentotus,* otherwise quite similar. Fertilisation duct short. Appended glands as in *C. hottentotus.* Bursa copulatrix of very characteristic shape, weakly sclerotised and externally covered by sclerotised platelets.
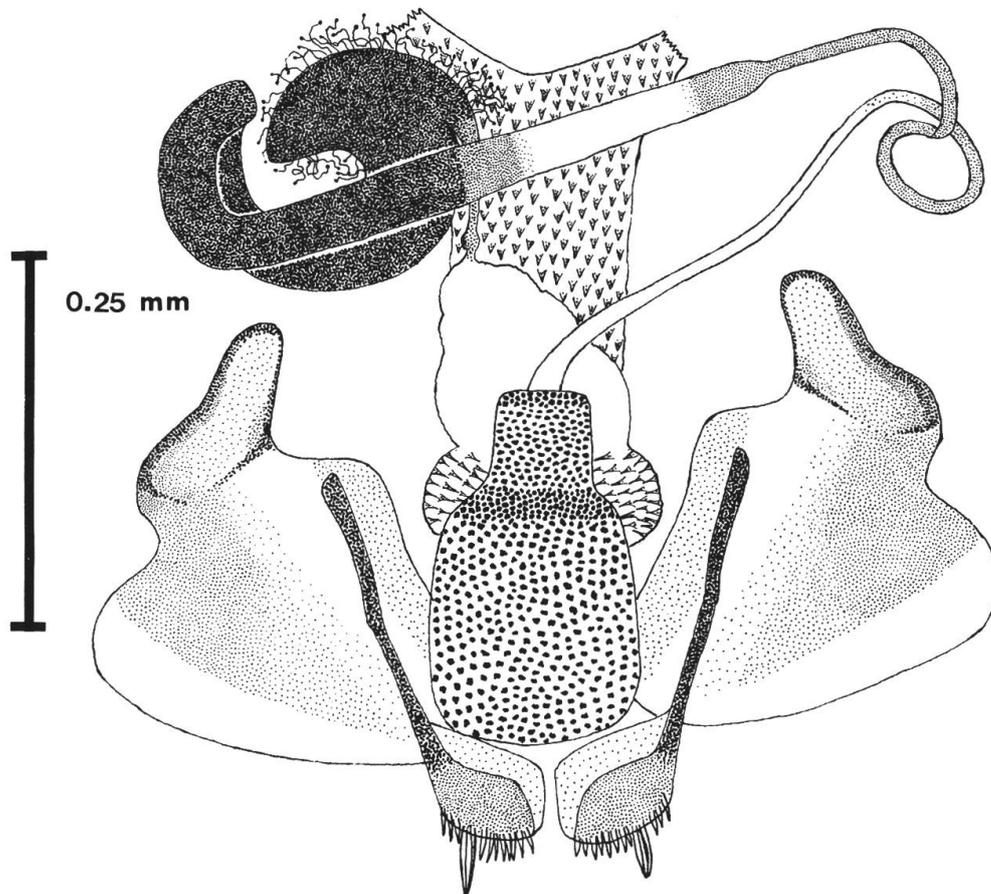
Fig. 6: Spermatheca and related organs in *Canthyporus petulans* Guignot.

Canthyporus consuetus J. Omer-Cooper Fig. 7.

Spermatheca as in *C. petulans,* but less strongly sclerotised (at least in the few specimens studied). Spermathecal duct much longer then in the two preceding species, coiled, weakly sclerotised. Appended glands as in the two preceding species. Bursa copulatrix non-sclerotised.
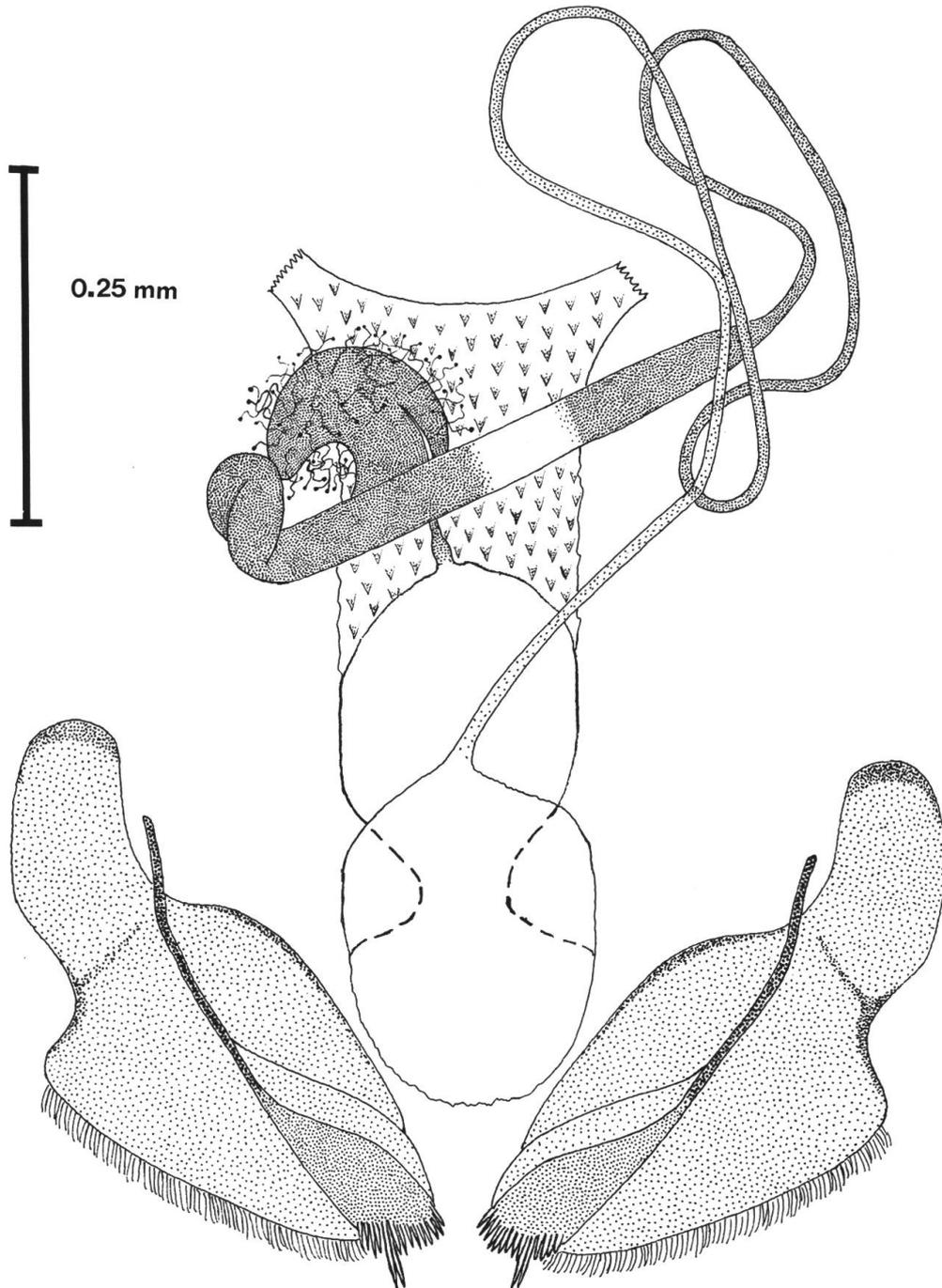
Fig. 7: Spermatheca and related organs in *Canthyporus consuetus* J. Om.-Coop.

Canthyporus lowryi J. Omer-Cooper   Fig. 8.

Female genitalia, except for minor differences, similar to those of *C. consuetus* (in the last 3 species the shape of the spermatheca is essentially identical, differences seen in the drawings are only due to slight differences in orientation and to intraspecific variations).

0.25 mm
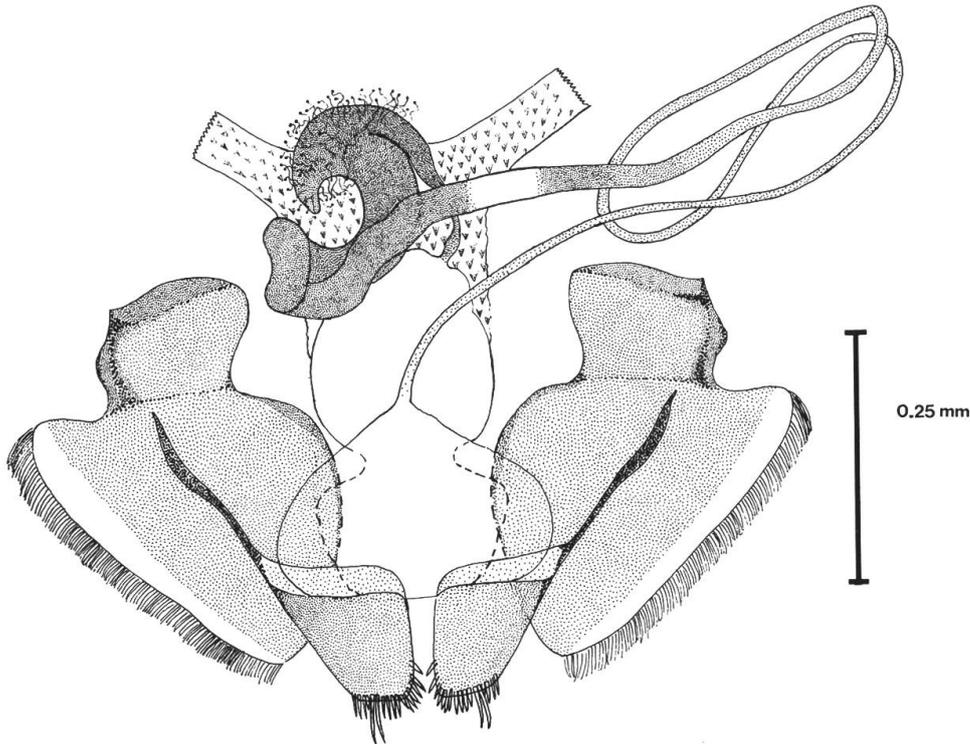
Fig. 8: Spermatheca and related organs in *Canthyporus lowryi* J. Om-Coop.

Canthyporus latus J. Omer-Cooper   Fig. 9.

Spermatheca moderately dilated and weakly sclerotised, with apical part covered by very large appended glands. Spermathecal duct very long and coiled. Bursa copulatrix small, triangular and non-sclerotised.

It is clear from consideration of the species mentioned above and from examination of the figures that it is possible to divide the species of *Canthyporus* studied into three different groups according to the characters of their spermathecae and related organs. The first groups includes *C. navigator* and *C. guignoti* and is characterized by a small, weakly sclerotised spermatheca with a very long and thin
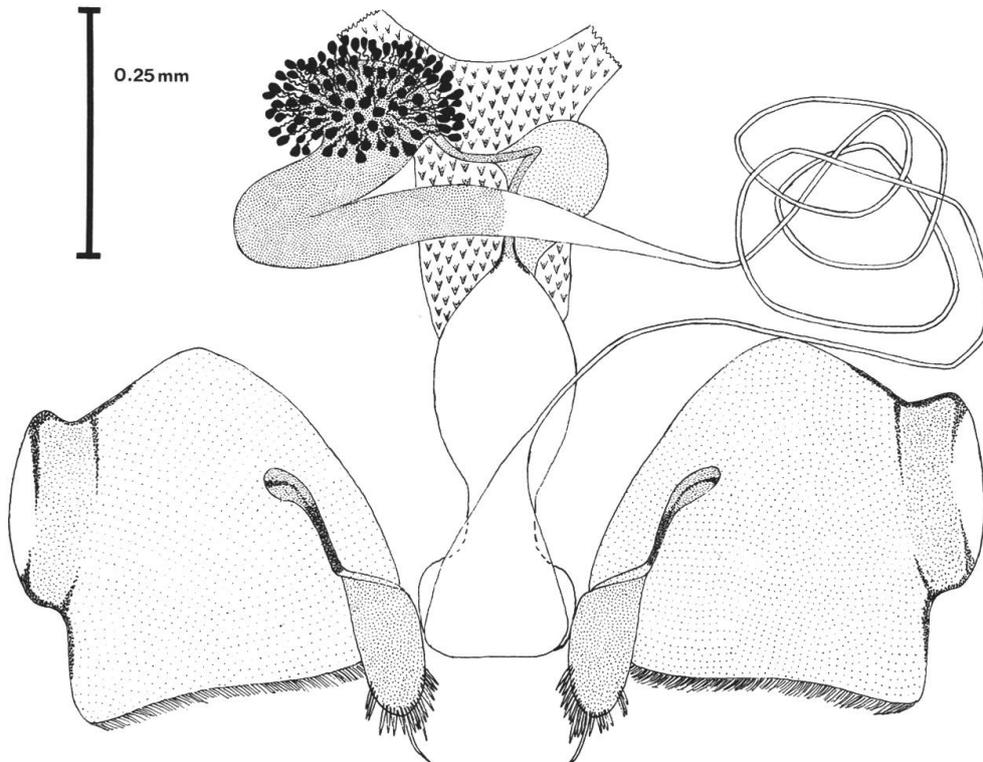
Fig. 9: Spermatheca and related organs in *Canthyporus latus* J. Om.-Coop.

spermathecal duct. The second group includes *C. canthydroides* and *C. testaceus,* and is characterized by a much larger, more dilated but still weakly sclerotised spermatheca, with a much shorter and thicker spermathecal duct. The third group includes *C. hottentotus, C. petulans, C. consuetus* and *C. lowryi,* and is characterized by a rather large, but not very dilated spermatheca, hook – shaped, with a spermathecal duct ranging from moderately short to moderately long, moderately to strongly coiled, of average thickness. Finally, *C. latus* (Fig. 9) presents a very interesting situation, as the spermatheca appears to be intermediate, in shape and size, between those of the first and second groups; the spermathecal duct is long, almost as long as in *C. guignoti* and *C. navigator,* while the appended glands are noticeably larger than in all the other species.

I feel that the structures described above may be phylogenetically significant at two separate levels, firstly with regard to the placement of *Canthyporus* within the Hydroporinae, and secondly for identifying phylogenetic trends within *Canthyporus* itself.
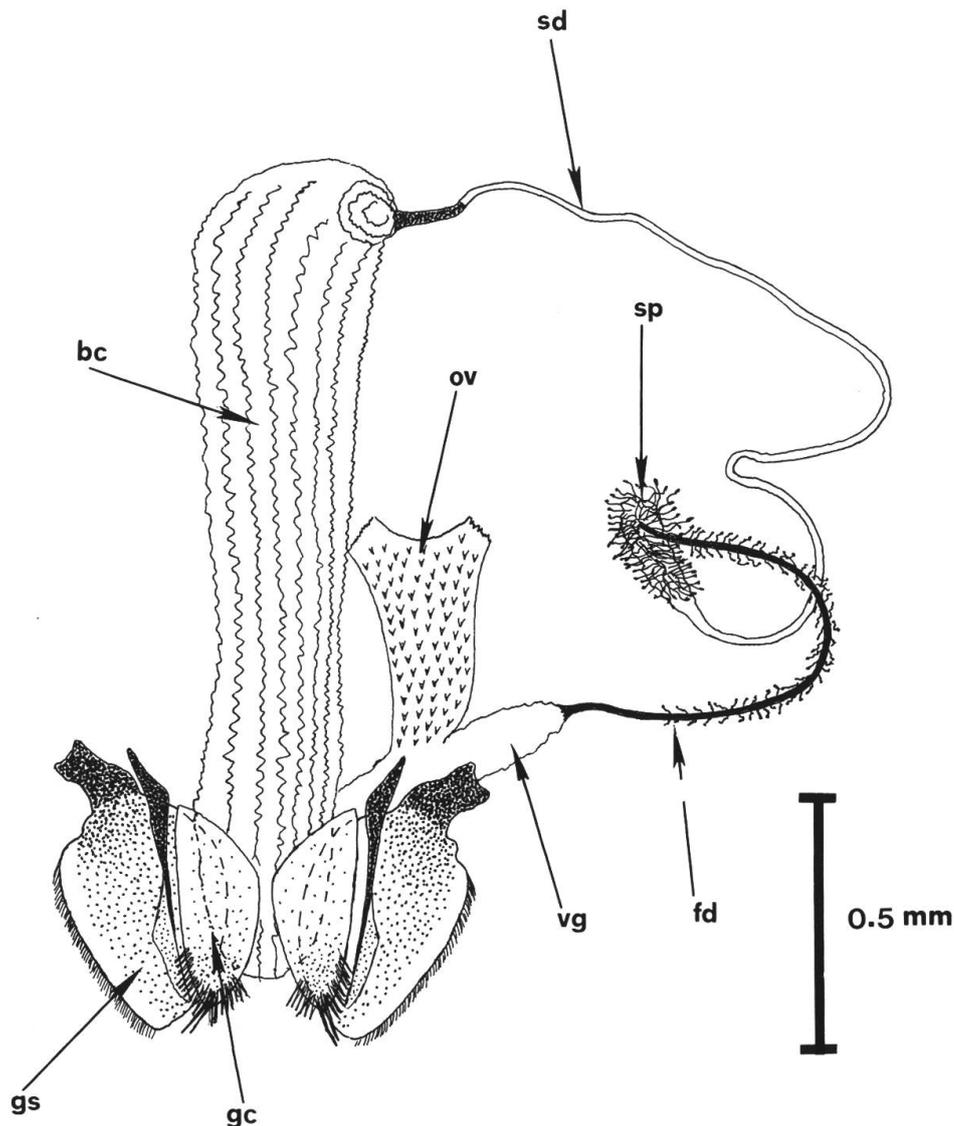
Fig. 10: Spermatheca and related organs in *Laccornis oblongus* (Steph.). Ov: oviduct; sp: spermatheca with appended glands; sd: spermathecal duct; fd: fertilisation duct; vg: vagina; bc: bursa copulatrix; gc: gonocoxae; gs: gonocoxosterna.

THE FEMALE GENITALIA AND THE PHYLOGENY OF HYDROPORINAE

ANGUS (1985), after examining the female genitalia in some genera of Hydroporinae, maintains that there are two "patterns" in this subfamily. The first is found in *Hydroporus* and is characterized by a large and muscular bursa copulatrix, a spermathecal duct so short to be virtually absent in most species and a spermatheca with a small basal diverticulum; the second is found in *Nebrioporus (= Potamo-*
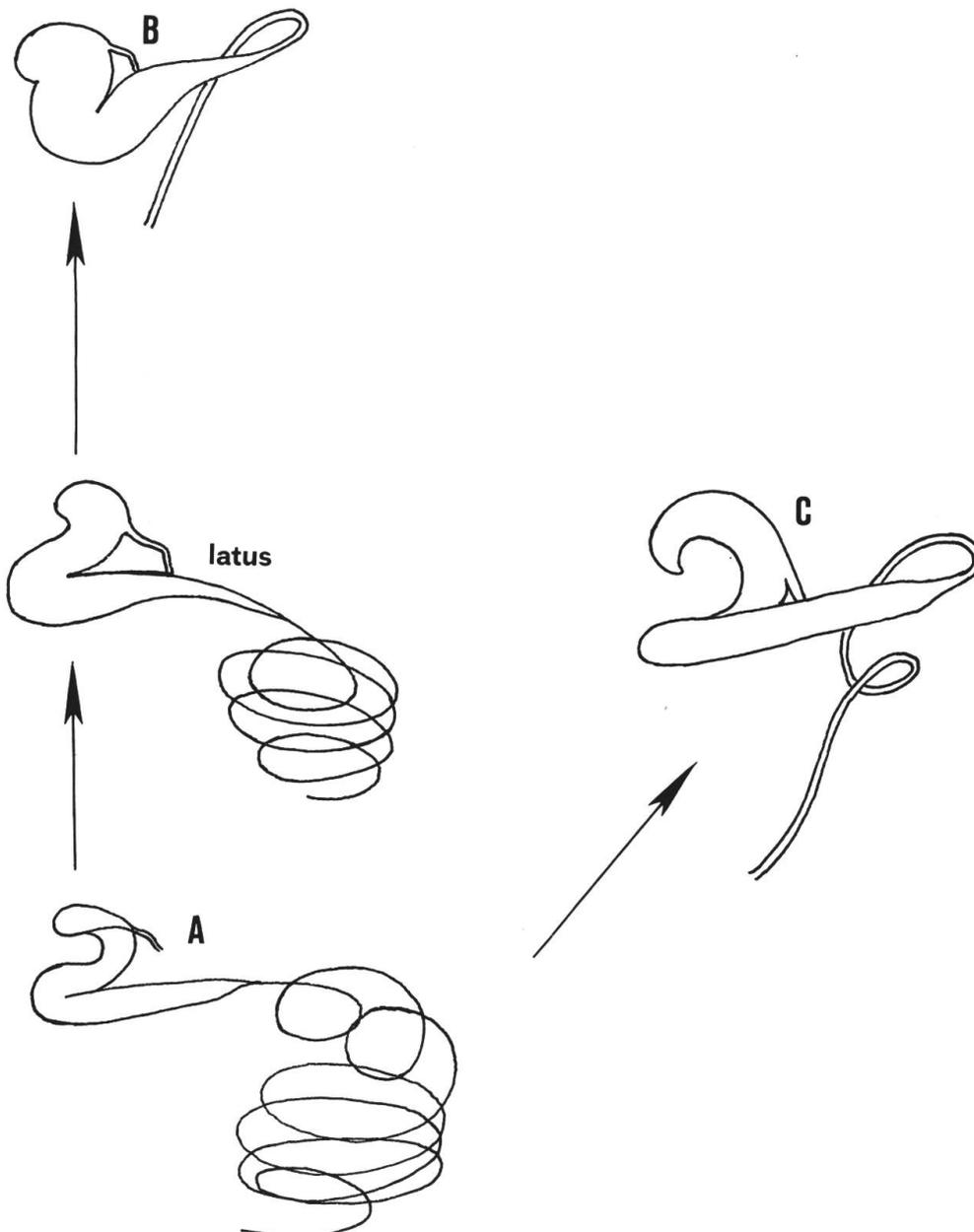
Fig. 11: Proposed evolution of the different types of spermatheca in *Canthyporus*.

nectes), *Stictotarsus*, *Scarodytes* and *Oreodytes* and is characterized by a small bursa copulatrix with feeble musculature, a long spermathecal duct and a bilobed spermatheca, one of the lobes being the diverticulum which is much larger than in *Hydroporus*. The situation seems more complex than ANGUS (1985) supposed, however, since the female genitalia of *Canthyporus,* for example, appear to be similar to those of *Nebrioporus* and related genera but with an important difference: the lack of a diverticulum.

P. Mazzoldi

Fig. 12: Phylogenetic tree of *Hydroporinae* and evolution of female genitalia; the circles represent the main events : 1) development of primitive, non sclerotised and small spermatheca; both spermathecal duct and fertilisation duct rather long; 2) sclerotisation of spermatheca; 3) secondary loss of sclerotisation of spermatheca; 4) presence of appended glands; 5) development of diverticulum; 6) reduction (almost loss) of spermathecal duct; 7) reduction of fertilisation duct

In order to understand the possible phylogenetic significance of these structures I have tried to reconstruct a phylogenetic tree of the Hydroporinae on the basis of the female genitalia; to this end I have utilized the characters of the genera considered by ANGUS (1985) (and as already mentioned I have myself dissected some of them in order to clarify some characters not mentioned by Angus); furthermore, I have examined the genitalia of *Copelatus caffer* Balfour-Browne, as this genus is considered by RUHNAU & BRANCUCCI (1984) to be the sister group of all the other Dytiscidae and therefore may serve as an outgroup for the analysis.

Of course it is not possible to carry out a complete cladistic analysis of Hydroporinae on the basis of the female genitalia alone, not only because for such an analysis all the characters should be considered, but also because I have been able to examine the female genitalia of a limited number of genera, and of single species within each genus. Therefore I simply propose a hypothetical phylogenetic tree based on the evolution of female genitalia, in the hope that this might be useful as a starting point for a more detailed analysis which should be possible when we know more about the structure of the female genitalia in a greater number of genera and species of Hydro-porinae and other Dytiscidae.

Discussion of characters

I accept as a basis for the analysis the phylogeny proposed by RUHNAU and BRANCUCCI (1984), who consider *Copelatus* as the sister group of all the Dytiscidae, with Hydroporinae branching off first after *Copelatus*. Therefore the Copelatini may be employed as outgroup in the analysis of Hydroporinae.

The characters of the female genitalia utilized for the analysis are taken from the work of ANGUS (1985) and in part from personal observations; they are summarized in Table 1. I give the following interpretation of these characters.

Spermatheca

We find a sclerotised spermatheca in *Copelatus* and in all the genera of Hydroporinae, with the exception of *Laccornis* in which the spermatheca is only a slight, non-sclerotised dilation of the spermathecal duct (Fig. 10). In all the species considered, including *Laccornis,* the spermatheca, or at least part of it, is covered by small glands, although these may vary greatly in number, being very numerous in some genera (e.g. *Copelatus*) and very few in others (e.g. *Celina*). The presence of these glands helps identify the spermatheca when, as in *Laccornis,* it is not evident morphologically. Although in the outgroup *(Copelatus)* we find a sclerotised spermatheca, I consi-der the condition in *Laccornis* the plesiomorphic one, as it appears logical to consider that the spermatheca must have evolved from a dilation of the spermathecal duct, and therefore I hypothesize that the sclerotisation of the spermatheca has arisen independently in the lines leading to the Copelatini and to the Hydroporinae. The presen-

ce of glands, on the other hand, seems to be a synapomorphy of at least the clade *Copelatus* + Hydroporinae, being present in all the members of this group (at least in the sense that this character might have a wider distribution in the Dytiscidae). It must be noted that the non-sclerotised spermatheca of *Hydroporus* must be considered an apomorphic condition in which the sclerotisation was secondarily lost, as this large spermatheca provided with diverticulum surely has no close relationship to the slight dilation of the genital duct found in *Laccornis*.

Diverticulum

A diverticulum is only present in some genera of Hydroporinae and is absent in all other genera and in *Copelatus*. I therefore consider the presence of a diverticulum the apomorphic condition, and its absence the plesiomorphic one. This structure is very peculiar, as it is characterized by the presence at the base of a strongly sclerotised ring; it appears therefore rather unlikely that it might have arisen independently in the different genera, hence I consider it a good synapomorphy of the group of species possessing it.

Oviduct

In both *Copelatus* and all the Hydroporinae examined the external surface of the common oviduct is covered by sclerotised spines, therefore this character must be considered a synapomorphy of at least the clade *Copelatus* + Hydroporinae , like the above mentioned spermathecal glands.

Fertilisation duct

The fertilisation duct appears relatively long in both *Laccornis* and *Copelatus,* while it is very short and sometimes completely absent in all the other genera. Therefore I consider a relatively long fertilisation duct as the plesiomorphic condition and a very reduced one as the apomorphic one.

Spermathecal duct

The spermathecal duct appears more difficult to interpret, as it varies rather strongly in the different genera and even within a single genus, as exemplified by *Canthyporus*. Nonetheless, it is relatively long in all the genera including *Copelatus,* and is very short only in *Hydroporus,* where it is pratically obliterated; I consider therefore the latter condition an autapomorphy of *Hydroporus,* and a relatively long duct a plesiomorphic condition.

TABLE 1

Species	Spermatheca	Appended glands	Diverticulum	Spermathecal duct	Fertilisation duct	Bursa copulatrix
Copelatus caffer Balfour-Browne	sclerotised, weakly dilated	present	absent	long	long	large, weakly sclerotised
Laccornis oblongus (Steph.)	small non-sclerotised, only slightly dilated	present	absent	long	long	large, weakly sclerotised
Celina angustata Aubé	weakly sclerotised, moderately dilated	present (but reduced, very few)	absent	long	short	large, weakly sclerotised
Hydrovatus pustulatus Melsh.	weakly sclerotised, weakly dilated	present	absent	moderately long	very short	medium-sized, non-sclerotised
Canthyporus spp.	sclerotised, weakly to moderately dilated	present	absent	moderately long to very long	very short	small, non-sclerotised to weakly sclerotised
Hydroglyphus pusillus (F.)	sclerotised, dilated	present	absent	long	very short	small to medium -sized, non or weakly sclerotised
Nebrioporus spp. (*suavis* (Sharp), *depressus* (F.) and *assimilis* (Payk.))	sclerotised, dilated	present	present	long	very short	small, non-sclerotised
Deronectes spp. (*latus* (Steph.), *moestus* (Fairm.) and *hispanicus* (Ros.))	sclerotised, dilated	present	present	long	very short	large, non-sclerotised to partially sclerotised
Suphrodytes dorsalis (F.)	weakly sclerotised, dilated	present	present	long	very short	large, elongated, but weakly sclerotised
Hydroporus spp. (many species, see Angus 1985, and *H. palustris* (L.))	non-sclerotised, strongly dilated	present	present	very short, almost obliterated, to short	very short	large, muscular

Table 1: Characters of female genitalia in some genera of Hydroporinae; data drawn from Angus (1985) and personal observations.

Bursa copulatrix

This character is even more difficult to interpret than the preceding one. The bursa is rather large and weakly sclerotised in *Copelatus, Laccornis* and *Celina,* while it is much smaller and non – sclerotised in most other genera, which could lead one to believe that a rather large bursa copulatrix is a plesiomorphic condition in Hydroporinae. There are, however, strong variations in size and sclerotisation within genera, as exemplified by *Canthyporus,* and we again find a very large bursa copulatrix in *Hydroporus,* which from the presence of the diverticulum cannot be considered a basal lineage within Hydroporinae. It is therefore evident that there must have been reversals and parallelisms in the development of this organ, making its use in phylogenetic analyses highly problematic.

TABLE 2

	1	2	3	4	5	6	7
Copelatus caffer Balf.-Br.	1	1	0	1	0	0	0
Laccornis oblongus (Steph.)	1	0	0	1	0	0	0
Celina angustata Aubé	1	1	0	1	0	0	1
Hydrovatus pustulatus Melsh.	1	1	0	1	0	0	1
Canthyporus spp.	1	1	0	1	0	0	1
Hydroglyphus pusillus (F.)	1	1	0	1	0	0	1
Nebrioporus spp.	1	1	0	1	1	0	1
Deronctes spp.	1	1	0	1	1	0	1
Suhrodytes dorsalis (F.)	1	1	0	1	1	0	1
Hydroporus spp.	1	1	1	1	1	1	1

Table 2: Data matrix of character states of female genitalia in some genera of Hydroporinae (0 plesiomorphic, 1 apomorphic)
1) presence of a differentiated spermatheca; 2) sclerotisation of spermatheca; 3) secondary loss of sclerotisation of spermatheca; 4) presence of appended glands; 5) presence of diverticulum; 6) spermathecal duct reduced; 7) fertilisation duct reduced.

The data contained in table 1 have been translated into the data matrix of table 2 and on its basis I have built a phylogenetic tree of the genera of Hydroporinae considered (see Fig. 12). I have not introduced in table 2 the bursa copulatrix, which was probably large and rather weakly sclerotised in the basal lineages of this clade, as the above mentioned parallelisms and reversals which this organ has undergone make it scarcely useful for analysis.

I hypothesize that the primitive female genitalia of the clade Copelatini + Hydroporinae were characterized by a small, weakly dilated, non sclerotised spermatheca provided with appended glands; the spermathecal duct and fertilisation duct were both long, coiled and non sclerotised; the bursa copulatrix was probably big and weakly sclerotised. Then the spermatheca underwent sclerotisation independently in the lines leading to Copelatini and Hydroporinae; in the latter line, after *Laccornis* branched off, the fertilisation duct underwent a strong reduction. As already mentioned, the development of the diverticulum is a synapomorphy shared by a group of advanced Hydroporinae, while *Hydroporus* seems to be characterized by two autapomorphies, that is the strong reduction of the
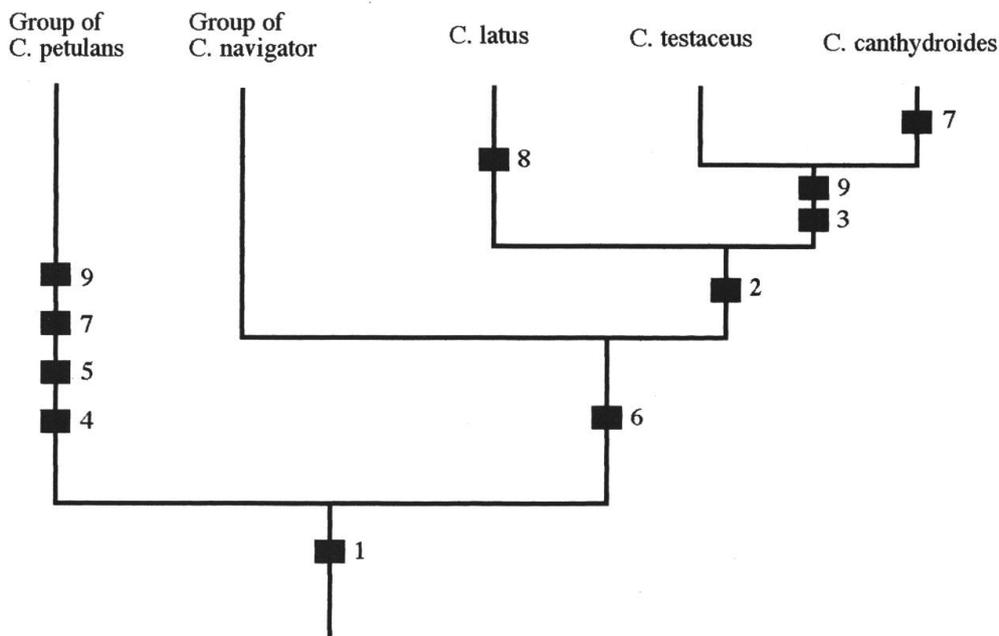

Fig. 13: Phylogenetic tree of the species of *Canthyporus* studied. The numbers indicate the character states: 1) spermatheca as in *C. navigator;* 2) spermatheca as in *C. latus;* 3) spermatheca as in C. canthydroides; 4) spermatheca as in *C. petulans;* 5) aedeagus with ventral projection; 6) parameres with apical incision; 7) presence of metasternal lines; 8) appended glands big; 9) reduction of spermathecal duct.

spermathecal duct and the development of a large muscular bursa copulatrix. Of course this tree must be considered with great caution, as the possibility that other homoplasies are present cannot be ruled out. The sclerotisation of the spermatheca for example could have evolved independently in various lineages.

The situation in *Suphrodytes* also deserves some comment. ANGUS (1985) separated it from *Hydroporus* (of which it was previously a subgenus), saying that in the structure of the female genitalia it was much closer to *Nebrioporus (= Potamonectes)* and related genera *(Oreodytes, Deronectes, Scarodytes* and *Stictotarsus)*, which have a long spermathecal duct and a small bursa copulatrix. In reality, the situation is not so clear – cut, since: 1) the spermathecal duct is long in *Suphrodytes,* but still much shorter than in *Nebrioporus* and related genera, and some *Hydroporus,* as Angus himself reports, have a slightly longer duct; 2) the bursa copulatrix is not really very small in *Suphrodytes,* and it is not always small in the group of genera near *Nebrioporus* (e.g. ANGUS (1985) quotes *Deronectes latus* amongst the species which have a small bursa, but in *D. hispanicus* and *D. moestus* the bursa is instead big, and in the second species even strongly sclerotised, at least in its distal part). Therefore, it seems to me that *Suphrodytes* cannot be included in the group of genera near *Nebrioporus,* but rather occupies an intermediate position between these genera and *Hydroporus*. This finding is a reminder of the fact that in order to draw reliable phylogenetic conclusions based on female genitalia we need to examine these structures in a wide range of genera and species.

Phylogenetic trends in Canthyporus

I have attempted to reconstruct a phylogenetic tree of the species studied taking into consideration both the female genitalia and some other characters exclusive to *Canthyporus* and subject to variation within the genus: 1) the presence of a characteristic projection on the ventral side of the aedeagus; 2) the presence of an incision at the apex of the parameres; 3) the presence of two longitudinal lines in the middle of the metasternum. If we accept the phylogenies proposed by WOLFE (1988) and RUHNAU & BRANCUCCI (1984), then *Copelatus* (which is the sister group to all Hydroporinae) *Laccornis,* Methlinae *(Celina)* and *Hydrovatus* (which are the basal lineages of Hydroporinae) can be considered outgroups for the analysis of *Canthyporus*.

Table 3 summarizes the characters considered, which I now proceed to discuss. Of course these results must be considered provisional, since a more reliable analysis will only be possible when we have studied the spermathecae of all the species of this genus.

Spermatheca

WOLFE (1988) considers *Laccornis* the sister group to all other Hydroporinae, therefore the condition which we find in this genus (see Fig. 10) should be the most primitive. Hence a small, non-sclerotised and weakly dilated spermatheca should be considered plesiomorphic and a large sclerotised one apomorphic. On this assumption I have tried to build a phylogenetic tree of the evolution of the spermatheca in *Canthyporus,* and I hypothesize that the phylogenetic correlations between the different spermathecae found in the species studied are those shown by figure 11: the spermathecae found in *C. guignoti* and *C. navigator* are the most primitive, being weakly sclerotised and hardly dilated. From these two lines diverge, one leading to the spermathecae of *C. canthydroides* and *C. testaceus* through the condition found in *C. latus* via a strong dilation of the spermatheca (while the sclerotisation remains weak), the other leading to the spermathecae of the group of species close to *C. hottentotus.* In this line the spermathecae become strongly sclerotised but weakly dilated and the presence of a non-sclerotised stretch interposed between two sclerotised ones seems to be a synapomorphy of this group of species.

Fertilisation duct

As already stated, in Hydroporinae a long fertilisation duct must be considered plesiomorphic and a short one apomorphic. This character is of little phylogenetic value within *Canthyporus* since it is short in all the species studied.

Spermathecal duct

This character is difficult to interpret. It is relatively long in *Copelatus, Laccornis* and Methlinae *(Celina),* leading one to believe that a long spermathecal duct is the plesiomorphic condition. This could be confirmed by the fact that in the species with the most primitive spermatheca *(C. guignoti* and *C. navigator)* it is extremely

long. Nonetheless this character is subject to variation even between closely related species (e.g. in the group of species of *C. petulans*), meaning that the presence of homoplasies cannot be ruled out.

Aedeagus

The presence of a projection on the ventral side of the aedeagus is exclusive to a group of *Canthyporus* species and is not found in any of the outgroups, therefore this condition must be considered apomorphic (some species of *Copelatus* have projections on the aedeagus, but they are on the dorsal side of this organ and therefore cannot be considered homologous with those of *Canthyporus*).

Parameres

The presence of an incision at the apex of the parameres is also exclusive to a group of *Canthyporus* species and must therefore be considered apomorphic (an incision in the parameres is also found in another genus of Hydroporinae *(Oreodytes)* but it is different in shape and orientation, so that it is very likely that the two evolved independently). The apomorphic condition in this and in the preceding character was already recognized by NILSSON (1991) who on the basis of these characters recognized two species groups.

Metasternal lines

The presence of two parallel longitudinal lines on the middle of the metasternum is exclusive to some *Canthyporus* species, therefore this condition too must be considered apomorphic.

Bursa copulatrix

I have not been able to employ this character in the analysis, as variations between the species are slight and mainly quantitative. What seems likely is that the triangular, weakly sclerotised bursa copulatrix of *C. hottentotus* and that of *C. petulans,* covered by sclerotised platelets, are autapomorphies of the two species.

On the basis of the above mentioned interpretation, the characters of the nine species of *Canthyporus* were translated into the matrix of character states in Table 3. Fig. 13 gives the phylogenetic tree derived from this matrix. It is possible to identify two lineages, one leading

TABLE 3

Character	1	2	3	4	5	6	7
Species							
C. navigator	0	0	0	0	0	1	0
C. guignoti	0	0	0	0	0	1	0
C. latus	1	1	0	0	0	1	0
C. canthydroides	1	1	1	0	0	1	1
C. testaceus	1	1	1	0	0	1	0
C. consuetus	1	0	0	1	1	0	1
C. petulans	1	0	0	1	1	0	1
C. hottentotus	1	0	0	1	1	0	1
C. lowryi	1	0	0	1	1	0	1

Distribution of character states in the species of *Canthyporus* studied:
1) spermatheca not as in *C. navigator;* 2) spermatheca as in *C. latus* or spermathecae derived from it; 3) spermatheca as in *C. canthydroides;* 4) spermatheca as in *C. petulans;* 5) appendix on aedeagus; 6) incision in parameres; 7) metasternal lines (0 = = plesiomorphic character; 1 = apomorphic character)

to the group of species near *C. petulans,* all characterized by the presence of ventral projections on the aedeagus and spermathecae similar to *C. petulans,* the other leading to the species with incision at the apex of par ameres. These groups are the same as those identified by NILSSON (1991), which are here confirmed from spermathecal data. The tree contains two homoplasies: 1) the metasternal lines, which seem to develop independently in the lineage of *C. petulans* and in *C. canthydroides;* 2) the length of the spermathecal duct, which seems to undergo a progressive parallel reduction in both groups of species.

Unfortunately, I could not study any species of the third group hypothesized by Nilsson, the one containing the supposedly more primitive species lacking both the projection on the aedeagus and the

incision at the apex of parameres. If the interpretation of spermathecal evolution presented in this paper is correct, then these species should have the most primitive female genitalia.

And finally a consideration on *Canthyporus sigillatus* (Guignot). This species was originally described as a *Laccornis* (GUIGNOT, 1955) in view of the fact that the projection on the aedeagus is subapical rather than basal, and so more similar to *Laccornis*. WEWALKA (1981), considering the parameres, which are more similar to those in *Canthyporus,* transferred the species to the latter genus, but NILSSON (op. cit.) again questions the generic placement of this species and suggests that the presence or absence of a valvifer might solve the problem, as this structure is a synapomorphy of *Laccornis*. As a result of this study, the spermatheca might offer a second criterion. If *sigillatus* is a *Canthyporus,* it should belong to the group of *C. petulans* and so it should have a spermatheca like those of the species in this group, while if it is a *Laccornis* it should have no sclerotised spermatheca (unless, of course, it happened to represent a third, undescribed genus!).

Acknowledgments

References

ANGUS, R. B. (1985): *Suphrodytes Des Gozis a valid genus, not a subgenus of Hydroporus Clairville (Coleoptera: Dytiscidae)*. Entomol.scand. *16 (3):* 269–275.

BAMEUL, F. (1990): *Le DMHF: un excellent milieu de montage en entomologie.* L'entomologiste *46:* 233–239.

BRANCUCCI, M. (1980): *Morphologie comparée, évolution et systématique des Canthari-dae (Insecta: Coleoptera).* Entomologica Basiliensia *5:* 215–388.

BURMEISTER, E.G. (1976): *Der Ovipositor der Hydradephaga (Coleoptera) und seine phylogenetische Bedeutung unter besonderer Berücksichtigung der Dytiscidae.* Zoomorphologie *85:* 164–257.

DEUVE, T. (1993): *L'abdomen et les génitalia des femelles de Coléoptères Adephaga.* Mémoires du Muséum National d'Histoire Naturelle, Paris *155:* 1–184.

FERY, H. (1992a): *Coelambus lagari* n.sp. *und Coelambus sanfilippoi n.sp. aus dem westlichen Mittelmeergebiet (Coleoptera: Dytiscidae).* Entomol. Z. *102(7):* 113–132.

FERY, H. (1992b): Revision der *saginatus*-Gruppe der Gattung *Coelambus* Thomson (Coleoptera: Dytiscidae). Linzer biol. Beitr. 24/1: 339–358.

GUIGNOT, F. (1959): *Révision des Hydrocanthares d'Afrique (Coleoptera Dytiscoidea). Deuxiéme partie.* Annales du Musèe Royal du Congo-Belge, Tervuren, Sci. Zool. *78:* 323–648.

NILSSON, A.N. (1991): *On the genus* Canthyporus *Zimmermann (Coleoptera, Dytiscidae), with a new species from the highlands of Ethiopia.* Aquatic Insects *13 (3):* 183–188.

OMER-COOPER, J. (1955): *Canthyporus lateralis* (Boheman) and further new Dytiscidae from the Cape province of South Africa. Proc. R. Entomol. Soc.London (B) *24:* 189–196.

OMER-COOPER, J. (1956): *Five new species of* Canthyporus *from South Africa.* J. ent. Soc. S. Afr. *9: 2,* 302–309.

OMER-COOPER, J. (1965): *Coleoptera: Dytiscidae. A review of the Dytiscidae of Southern Africa being the results of the Lund University Expedition 1950–1951, with which are incorporated all other records known to the author.* In: South African Animal Life *11.* Chapter 2: 59–214 (Lund).

ORDISH, R.G., (1985): *A review of spermathecal structure in New Zealand dytiscids.* Proc. Acad. Nat. Sci. Philad. 137 (1): 128–131.

RUHNAU, S. & BRANCUCCI, M. (1984): *Studies on the genus Lancetes. 2. Analysis of its phylogenetic position using preimaginal characters (Coleoptera, Dytiscidae).* Entomologica Basiliensia *9:* 80–107.

WEWALKA, G. (1981): *Die Arten der Gattung* Canthyporus *Zimmermann aus Zentral- -Afrika mit Beschreibung einer neuen art (Dytiscidae, Col.).* Koleopterologische Rundschau *55:* 57–64.

WOLFE, G.W. (1988): *A phylogenetic investigation of* Hydrovatus, Methlini *and other plesiotypic hydroporines (Coleoptera: Dytiscidae).* Psyche *95 (3–4):* 327–344.

Author's address:
Paolo Mazzoldi
Via G.Galilei 87
I-25128 Brescia
Italy